

The Expanded Mandibular Condyle of the Megaladapidae

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KEY WORDS temporomandibular joint; mandibular symphysis; mastication; *Megaladapis*; Adapidae

ABSTRACT The Megaladapidae have a posterior expansion of the articular surface of the mandibular condyle. Several other strepsirhine species exhibit a similar condylar surface. In this study, I propose two behavioral scenarios in which the posterior articular expansion might function: 1) contact with the postglenoid process and resistance to joint stress during browsing, and 2) movement against the postglenoid process during the fast closing and power strokes of mastication, as a consequence of large transverse jaw movements and associated with a strong mandibular symphysis. These models are evaluated through dissection of the TMJ in *Lepilemur* and from comparative anatomical observations on strepsirhines and ungulates. In *Lepilemur* the mandibular symphysis is unfused, but compared to the unfused symphyses of other strepsirhines is strengthened by interlocking bony projections (Beecher [1977] Am. J. Phys. Anthropol. 47:325–336). An accessory articular meniscus is found between the posterior articular expansion and the postglenoid process in *Lepilemur*, suggesting that significant movement occurs in this part of the TMJ. The symphysis is fused in adult specimens of *Megaladapis*. A posterior articular expansion is common among ungulates, and its presence is associated not with browsing but with symphyseal fusion. This supports the second model and suggests that the posterior articular expansion functions as a movement surface during mastication. Schwartz and Tattersall ([1987] J. Hum. Evol. 16:23–40) cite the posterior articular expansion as a synapomorphy uniting an *Adapis-Leptadapis* clade with a Megaladapidae-*Daubentonina*-Indridae clade. The comparative evidence suggests that the posterior articular expansion has evolved convergently in adapines, notharctines, megaladapids, haplemurids, and indrids as part of a functional complex related to herbivory. However, close morphological similarity of the posterior articular expansion among genera within these strepsirhine subfamilies and families indicates that it is probably a reliable synapomorphy at lower taxonomic levels. Am J Phys Anthropol 103:263–276, 1997.

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The family Megaladapidae contains one extant genus, *Lepilemur*, and the recently extinct, subfossil genus *Megaladapis* (Tattersall, 1982). Although *Lepilemur* and *Megaladapis* differ by an order of magnitude in body mass (Jungers, 1991; Vuillaume-Randriamanantena et al., 1992) and in many aspects of their postcranial skeleton (Walker, 1967; Jungers, 1976), several features of the feeding apparatus are widely accepted as

synapomorphies (Tattersall and Schwartz, 1974; Szalay and Delson, 1979). For example, they share the highly derived condi-

Contract grant sponsor: National Science Foundation; contract grant number NSF BNS-8911315.

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Received 6 February 1996; revised 10 December 1996; accepted 26 March 1997.

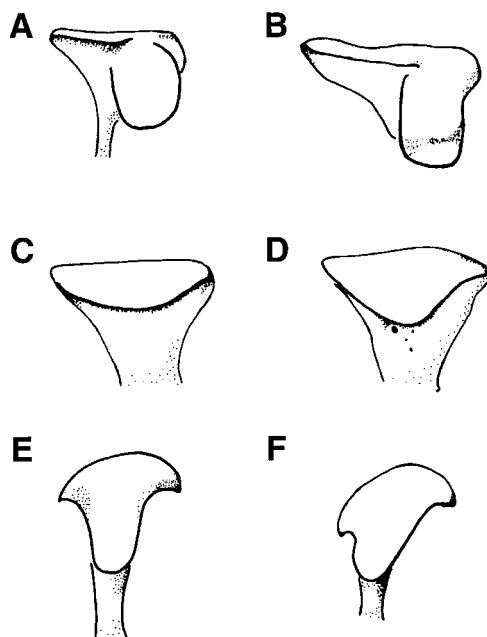


Fig. 1. Posterior view of mandibular condyle showing the posterior articular expansion. The left side is pictured; medial is to the right and superior toward the top. **A:** *Lepilemur leucopus*. **B:** *Megaladapis edwardsi* (AMNH 30025). **C:** *Eulemur fulvus*. **D:** *Papio* sp. **E:** *Propithecus verreauxi*. **F:** *Avahi laniger*.

tion among primates of loss of the maxillary incisors. They also possess nearly identical postcanine teeth (see Tattersall and Schwartz, 1974, and Schwartz and Tattersall, 1985, for specific characters), and an unusual configuration of the temporomandibular joint (TMJ).

Tattersall and Schwartz (1974:145) describe a "definite articular surface" descending medial to the posterior aspect of the condylar neck (Fig. 1). I refer to this feature as the posterior articular expansion. In addition, the anterior surface of the postglenoid process has a large, well defined articular facet which I refer to as the postglenoid facet (Fig. 2).

In most strepsirrhines, the condyle lacks a posterior articular expansion, and the postglenoid process does not have an articular facet (Figs. 1 and 2). Although the condylar articular surface extends onto the posterior aspect of the condylar process in a number of anthropoids, there is not a corre-

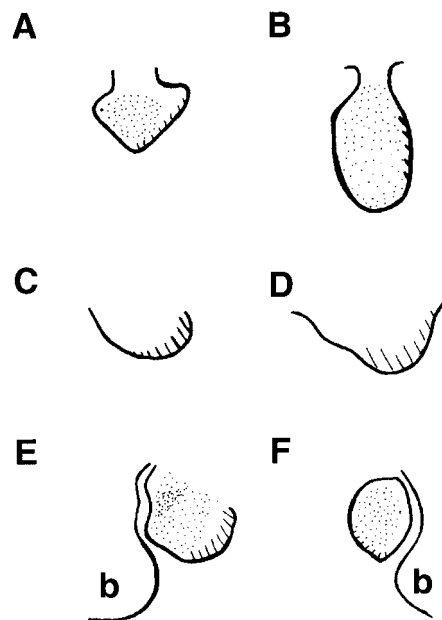


Fig. 2. The postglenoid process. Hatch marks = attachment site of the postglenoid ligament. Stippling = articular facet. b = auditory bulla. **A:** *Lepilemur leucopus*, left side, anterior view with medial to the left. **B:** *Megaladapis edwardsi* (AMNH 30024), left side, anterior view with medial to the left. **C:** *Eulemur* sp., left side, anteroventral view with medial to the left. **D:** *Papio* sp., left side, anteroventral view with medial to the left. **E:** *Propithecus verreauxi*, left side, anterolateral view with medial to the left. **F:** *Avahi laniger*, right side, anteroventral view with medial to the right. Note that an articular facet is present in *Lepilemur*, *Megaladapis*, *Propithecus*, and *Avahi*. The facet is absent in *Eulemur* and *Papio*. The space between the postglenoid process and the auditory bulla is exaggerated in E and F.

sponding articular facet on the postglenoid process (Figs. 1 and 2). However, a posterior articular expansion and a postglenoid facet are found in the extant indrids and also frequently in *Hapalemur* (Figs. 1, 2, and 3). As shown in Figure 1, in the indrids, the posterior articular expansion extends onto the posterior aspect of the condylar neck itself (Tattersall and Schwartz, 1974).

The posterior articular expansion may be related functionally to herbivory. The diet of *Lepilemur* consists primarily of leaves (Hladik and Charles-Dominique, 1974), and herbivory has been inferred for *Megaladapis* on the basis of dental and cranial anatomy and dental microwear (Tattersall, 1972, 1975, 1978; Rafferty and Teaford, 1992). The in-

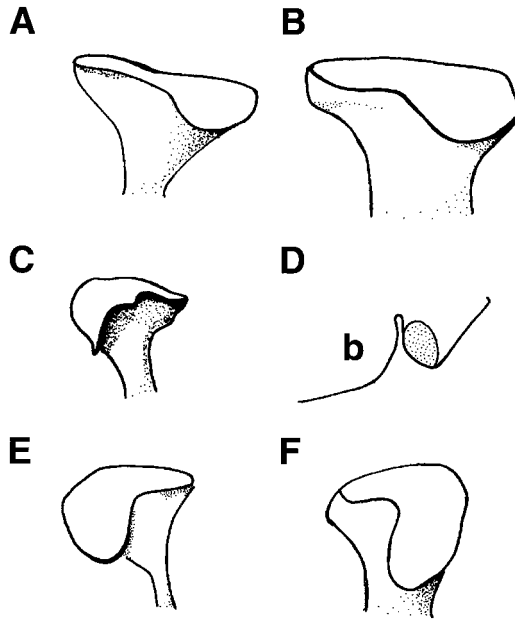


Fig. 3. TMJ articular surfaces of *Hapalemur* and fossil strepsirhines. **A:** *Hapalemur griseus*, posterior view of left condyle with medial to the right. **B:** *Leptadapis magnus* (cast, Paris Quarry 10893), posterior view of left condyle with medial to the right. **C:** *Smilodectes gracilis* (USNM 25686), posterior view of right condyle with medial to the left. **D:** *Smilodectes gracilis* (USNM 21815), anterior view of left postglenoid process with medial to the left. **b** = auditory bulla. **E:** *Notharctus tenebrosus* (USNM 21968), posterior view of right condyle with medial to the right. **F:** *Notharctus robustior* (USNM 21980), posterior view of left condyle with medial to the left. Superior is toward the top.

drids also specialize on leaves (Richard, 1985). Hill (1953) described articular tissue covering the bony surfaces of the posterior articular expansion and the postglenoid facet in extant indrids and *Lepilemur*. Hill (1953) thought that *Propithecus diadema* showed the most specialized TMJ, one that permits a wide range of transverse jaw movement during leaf mastication. A posterior articular expansion has also been described in some ungulates (e.g., Fortelius, 1985). This is particularly intriguing because ungulates and *Megaladapis* share other features of cranial anatomy that appear to be functionally related to herbivory (Table 1).

Schwartz and Tattersall (1979, 1985, 1987) note that *Adapis* and *Leptadapis* have a posterior articular expansion similar to that of the megaladapids and the extant indrids

(Figs. 1 and 3). They identify the posterior articular expansion as a synapomorphy uniting an *Adapis-Leptadapis* clade with a Megaladapidae-*Daubentonia*-Indridae clade.¹ However, the function of the posterior articular expansion has not been considered in discussions of strepsirhine interrelationships. For example, Schwartz and Tattersall (1979, 1985, 1987) did not discuss the possibility of convergence as an explanation for the presence of a posterior articular expansion in *Adapis*, *Leptadapis*, indrids, and megaladapids, nor did they consider the implications of the presence of this trait in *Hapalemur* and some notharctines.

In this study, I further describe the anatomy of the posterior part of the TMJ in megaladapids to determine the function of this region during feeding. I formulate two biomechanical models of how the posterior articular expansion works. The first proposes a function for the posterior articular expansion during ingestion, and the second proposes a function during mastication. These models are evaluated from comparative anatomical observations made on ungulates and primates. A major part of this comparison is a survey of the distribution of the posterior articular expansion in these two groups. The anatomical observations also allow an evaluation of the likelihood of convergence in TMJ morphology between adapines, notharctines, indrids, hapalemurids, and megaladapids.

BIOMECHANICAL MODELS

Browsing model

Browsers usually eat leaves and fruits that they pluck selectively from the available herbage. This is in contrast to grazers, which tend to indiscriminately crop primarily grasses. The comparative work of Tattersall (1972, 1975, 1978) demonstrated a suite of convergent adaptations in the crania of *Megaladapis*, some browsing ungulates, and the koala bear (*Phascolarctos cinereus*) (Table 1). These convergent features and the shearing design of the postcanine teeth suggested a specialized browsing-via-plucking mode of ingestion for *Megaladapis* (Tatter-

¹*Daubentonia* lacks a posterior articular expansion.

TABLE 1. Some anatomical convergences seen in *Megaladapis*

Convergence	Functional explanation
<i>Megaladapis</i> and Ungulata (Tattersall, 1972)	Tattersall (1972) proposes that these features are adaptations to browsing in <i>Megaladapis</i> . Features 2 and 3 suggest the presence of a horny pad for cropping leaves. The diastema may be used as an area for positioning leaves for transport to the postcanine dentition (De Vree and Gans, 1975; Osborn, 1981).
1. C/P ² diastema	
2. Loss of maxillary incisors (Bovidae)	
3. Elongate, ventrally flexed nasal bones (some tay-assuids)	
<i>Megaladapis</i> and the koala bear (<i>Phascolarctos cinereus</i>)	Tattersall (1972) identifies Features 4 and 5 as a functional complex that effectively turns the head into an extension of the neck. This adaptation increases the radius of movement of the mouth so that greater quantities of leaves can be procured from a single location in a tree.
4. Airorhynchus or ventral flexion of face (Hofer, 1952)	
5. Caudal orientation of foramen magnum (Tattersall, 1972)	
6. Trunk held in an upright position (Walker, 1967)	Features 6 and 7, and many other postcranial features unique to <i>Megaladapis</i> (see Jungers, 1976) support Tattersall's (1972) interpretation because they indicate that <i>Megaladapis</i> was arboreal, preferred vertical supports, and was a slow climber.
7. Habitual flexion of hip and knee (Jungers, 1976)	

sall, 1972). Both *Lepilemur* and *Avahi* have been observed to browse (Hladik and Charles-Dominique, 1974; Albignac, 1981).

In the browsing model (Fig. 4), because leaves and stems are relatively flat, plucking occurs when the mouth is closed and the posterior articular expansion is near or in contact with the postglenoid process. It is proposed that plucking is associated with activity in the posterior temporalis muscle.² This muscle was quite large in *Megaladapis* (Tattersall, 1973). The posterior force component of the posterior temporalis muscle causes the posterior articular expansion to contact the anterior surface of the postglenoid process, which acts as a brace. This generates a compressive reaction force in the posterior part of the TMJ which is resisted by the posterior articular expansion. The browsing model predicts that browsers will have a posterior articular expansion and a posterior joint contact that are well developed.

An alternative to this model is that the force used to pluck food items comes from the neck musculature during upward and/or backward head movements. Such behaviors have been observed in goats (De Vree and Gans, 1975). In this case, plucking activities may be associated with primarily vertical muscle forces acting on the mandible. These vertical forces resist the tendency of the food

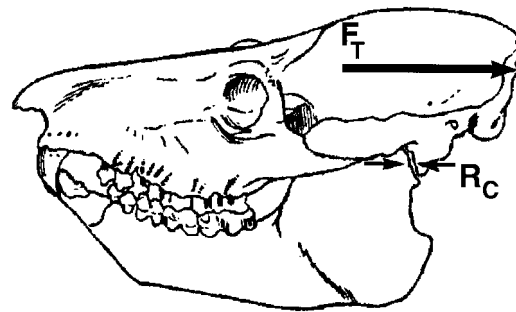


Fig. 4. Browsing model. Flat or small diameter food items are held at the front of the mouth by vertical muscle force (not illustrated), and they are pulled from plant stems by posterior muscle force. The posterior force component of the posterior temporalis muscle (F_T) causes a compressive reaction force (R_C) in the posterior part of the TMJ at the posterior joint contact. The magnitudes of the F_T and R_C are unknown, and here are drawn to arbitrary magnitudes. The cranium of *Megaladapis* is redrawn from Tattersall (1978).

item to dislocate anteriorly. A posterior joint contact is not necessary because there is no reaction force in the posterior part of the TMJ.

Transverse movement during mastication model

The chewing cycle of herbivorous ungulates is characterized by marked transverse movement of the lower jaw relative to the upper jaw (Becht, 1953; Crompton and Lieberman, 1995; De Vree and Gans, 1975; Greaves, 1980; Hildebrand, 1937; Janis,

²Other adductor muscles may be active but do not have a posterior force component.

1979; Lieberman and Crompton, 1996). During the fast closing stroke, the working side of the mandible moves laterally away from the midline. This brings the buccal edges of the lower teeth into alignment with those of the upper teeth. During the power stroke, the working-side lower teeth move medially toward the midline as they shear against the upper teeth. The postcanine teeth of herbivorous ungulates and megaladapids are strongly anisodontic (i.e., the maxillary molars are much wider buccolingually than the mandibular molars; Fortelius, 1985) and have enamel ridges that act as shearing edges during transverse jaw movements. These structural similarities suggest that megaladapids also emphasize transverse jaw movements during the power stroke.

Although the precise pattern of condylar motion is not fully documented, a number of researchers have proposed that in ungulates the posterior surface of the condyle contacts the anterior surface of the postglenoid process during mastication (Crompton and Lieberman, 1995; Fortelius, 1985; Greaves, 1972, 1980; Murphy, 1956; Weijs, 1994; Lieberman and Crompton, 1996, personal communication from D.E. Lieberman).

The transverse movement model is based on the idea that enlarged articular surfaces will develop in the posterior TMJ when there is increased condylar motion during mastication. Increased condylar motion causes the condyle to slide and rotate against the postglenoid process and is due to relatively large transverse jaw movements during the fast closing and power strokes of mastication.

In this model, increased transverse jaw movement toward the working side during fast closing causes the posterior articular expansion of the working-side condyle to first contact and then move against the postglenoid facet (Fig. 5). Likewise, increased transverse movement toward the balancing side during the power stroke causes the posterior articular expansion of the balancing-side condyle to first contact and then move against the postglenoid facet (Fig. 5). The movement of the balancing-side condyle may be greater than that on the working side since transverse jaw move-

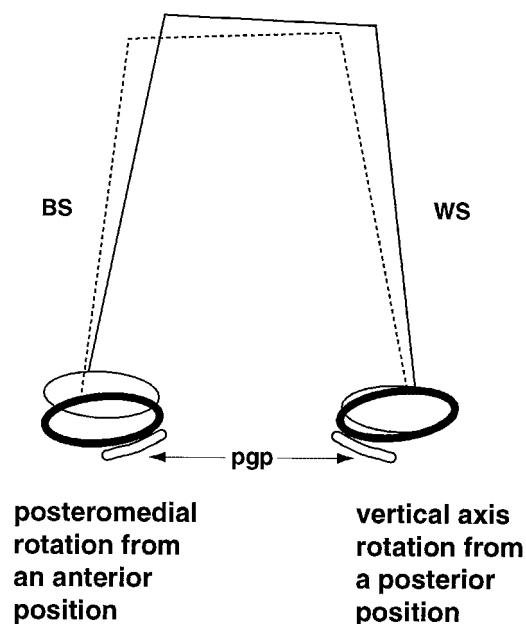


Fig. 5. Transverse movement model shown in this schematic, occlusal view of the lower jaw. BS = balancing side, WS = working side, pgp = postglenoid process. The starting condylar positions (solid jaw outlines, light condylar outlines) take place at maximum gape. Both condyles are forward in the glenoid fossa and the lower jaw is rotated slightly toward the working side. During the fast closing stroke (not shown), the balancing-side condyle rotates clockwise about a vertical axis toward the working side. The postcanine teeth move into buccal alignment, and the posterior articular expansion of the working-side condyle contacts and moves against the postglenoid process in the later part of the stroke. At the end of fast closing, both condyles are located posteriorly in the joint, and the balancing-side condyle is close to contact with the postglenoid process. During the power stroke (dashed jaw outlines, heavy condylar outlines), the working-side condyle rotates counterclockwise about a vertical axis at its contact with the postglenoid process. The mandibular molars are sheared against the maxillary molars, and the posterior articular expansion of the balancing-side condyle moves posterolaterally against the postglenoid process during most of the power stroke.

ment is probably greater during the power stroke than during fast closing.

The model proposes that larger transverse jaw movements are produced by increasing the adductor muscle force. Weijs (1994) summarizes experimental data suggesting that in ungulates the working-side posterior temporalis and the balancing-side medial pterygoid and superficial masseter muscles move the mandible toward the working side during fast closing. During the

power stroke, the balancing-side temporalis and the working-side medial pterygoid and superficial masseter muscles move the mandible toward the balancing side. The muscles that cause these movements are referred to as triplet I and triplet II, respectively (see also Herring, 1992). One way to increase adductor force is to increase the force output of triplet I during fast closing and of triplet II during the power stroke. This will increase transverse jaw movement by increasing the vertical axis rotation of the mandible. When the occlusal plane is angled buccolingually, vertical muscle force relative to the transverse plane also contributes to transverse force acting at the occlusal plane (Becht, 1953; Greaves, 1980). However, this effect is limited to certain jaw positions during the fast closing and power strokes. A third option is to increase the force output of the adductor muscles that have predominately transverse force components during fast closing and the power stroke (e.g., the deep masseter) (Weijs, 1994; Hylander and Johnson, 1994).

A strong mandibular symphysis is required to resist the higher anteroposterior shear, dorsoventral shear, and transverse bending stresses caused by increased adductor muscle force (Beecher, 1977, 1979; Hylander, 1975, 1977, 1979a,b, 1984, 1985; Ravosa, 1991; Ravosa and Hylander, 1994). Therefore, this model predicts an association between symphyseal morphology and the morphology of the TMJ.

Since bone is stronger than fibrocartilage, a relatively strong symphysis is usually, though not always, completely or partially fused. The presence of interlocking bony shelves, as seen in *Lepilemur* (Beecher, 1977), also results in a stronger joint. The bony shelves enhance resistance to dorsoventral and anteroposterior shear stress and provide some resistance to transverse bending stress (Beecher, 1977).

This model predicts that an herbivore with a strong symphysis will also possess a posterior articular expansion and a postglenoid facet.

Evaluation of the models

The browsing model proposes contact between the posterior articular expansion and

TABLE 2. *Megaladapid comparative skeletal sample*

Species	Sample size	Museum or specimen number
<i>Lepilemur leucopus</i>	24	AMNH
<i>L. ruficaudatus</i>	4	AMNH
<i>Megaladapis</i>		
<i>madagascariensis</i>	1	AM display
<i>M. grandidieri</i>	2	AM "A," AM 6067
<i>M. edwardsi</i>	20	¹

¹ AM display, Beloha, Beavoha, 1846-4, 6000, 6001, 6003, 6014, 6035, 6047, 6071, 6104, 6106, 6159, 6161, and 6166; Vienna V1, V2b; AMNH 171171, 30025.

AMNH, American Museum of Natural History, Mammalogy; AM, Académie Malgaches (all 6000 series specimens housed currently at L'Université de Antananarivo); Vienna, Naturhistorisches Museum, Vienna, Austria.

the postglenoid facet. Although contact occurs in the transverse movement model, the important role for the posterior articular expansion and the postglenoid facet is that of a movement surface. Further, each model explains function during a distinct behavior. The browsing model is evaluated by comparing TMJ form in ungulates that browse and in those that graze to that of *Lepilemur*, *Megaladapis*, and other strepsirrhine primates. The transverse movement model is evaluated by comparing TMJ and symphyseal form in *Lepilemur*, *Megaladapis*, and other strepsirrhine primates to the TMJs of ungulates that have fused and unfused symphyses.

MATERIALS AND METHODS

The TMJ was dissected in two preserved, adult specimens of *Lepilemur* (AMNH 2279 and DUCP "1"). The skeletal sample used to describe the megaladapid TMJ is listed in Table 2. Two measurements were taken on the skeletal sample: 1) length of the posterior articular expansion (maximum dorsoventral extent of subchondral bone) and 2) width of the posterior articular expansion (maximum mediolateral extent of subchondral bone).

Descriptions of TMJ and symphyseal morphology in the extant primates and ungulates were made from adult specimens housed at the American Museum of Natural History (AMNH), the United States National Museum (USNM), the Department of Anatomical Sciences, SUNY at Stony Brook (SUNY-SB), and the Department of Biological Anthropology and Anatomy, Duke Univer-

sity (DU). Specimens of the fossil adapid primate species *Cantius venticolis* (AMNH 14656), *Smilodectes gracilis* (USNM 21815, 25686, and 33-67), *Notharctus tenebrosus* (AMNH 11466a, 127167, and 93617, USNM 21864 and 21968), *N. robustior* (USNM 21980), *Adapis parisiensis* (AMNH 98203 and 99982), and *Leptadapis magnus* (MNHM 10893) were examined at the AMNH and the USNM.

Data on feeding behavior and diet for the ungulates were taken from Janis and Ehrhardt (1988 and references therein) and Nowak (1991). Data on feeding behavior and diet for the primates were taken from Covert (1986), Fleagle (1988 and references therein), Hladik and Charles-Dominique (1974), Tattersall (1982 and references therein), and Richard (1985).

To categorize relative symphyseal strength in the strepsirhines and in the comparative sample of ungulates, Beecher's (1977, 1983), Scapino's (1981), and Ravosa's (1996) classifications were used in combination with personal observations. The key point in the classification adopted here is the degree of relative symphyseal strength. In this study, a symphysis was considered to be fused if the dentaries could not be separated into two elements (e.g., most adult indrid specimens) and functionally fused if interlocking bony or ligamentous structures were extensive (e.g., *Lepilemur*).

The maximum likelihood chi-square test of independence (Proc freq, SAS Institute Inc., 1988) was used to gauge the strength of association between the morphology of the posterior TMJ and either mode of ingestion or symphyseal strength in the ungulate sample, the extant strepsirhines, and *Megaladapis*. The adapids were not included in the statistical analysis because mode of ingestion could not be reliably inferred. Scores for each trait were assigned by family except when there was variation in the development of the posterior articular expansion within a family. A score of 1 was given for "fused/functionally fused symphysis," "browsing," and "presence of a posterior articular expansion." A score of 2 was given for "unfused symphysis," "grazing," and "absence of a posterior articular expansion." A score of 3 was given for posterior TMJ morphology

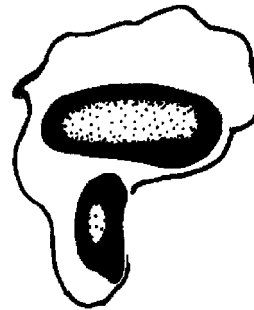


Fig. 6. The articular meniscus and the accessory articular meniscus in *Lepilemur* (DUPC "1," right side, superior view). The circumferential annuli of the menisci are in heavy outlines, and the intermediate zone is stippled. Medial is to the left, anterior is toward the top.

when the posterior articular expansion showed intermediate development (e.g., tapirids) or the postglenoid process was reduced in size (e.g., suids). A score of 4 was given for mode of ingestion when there was variation within the group (e.g., Rhinocerotidae) or when members of the group were neither grazers nor browsers.

RESULTS

The gross dissections of *Lepilemur* sp. revealed that a thick articular tissue lines both the posterior articular expansion of the condyle and the anterior surface of the postglenoid process. An accessory articular meniscus composed of dense fibrous material and connected to the articular meniscus was interposed between the posterior articular expansion and the postglenoid facet (Fig. 6).

Summary statistics of the dimensions of the posterior articular expansion in *Lepilemur* and *Megaladapis* are given in Table 3. In both genera, the posterior articular expansion is oriented nearly parallel to the coronal plane and is continuous with the superior articular surface of the condyle. Its shape is roughly rectangular (Fig. 1), and it meets the superior surface of the condyle at an angle of about 90 degrees. The expansion is slightly concave in *Lepilemur* and moderately concave in *Megaladapis*. There are subtle differences in the shape of the posterior articular expansion between the two genera (Table 3 and Fig. 1).

TABLE 3. The superoinferior length and mediolateral width¹ of the posterior articular expansion in *Lepilemur* and *Megaladapis*

Species	Posterior expansion length			Posterior expansion width		
	N	Mean	SD	N	Mean	SD
<i>Lepilemur leucopus</i>	24	2.46	0.28	24	2.07	0.17
<i>L. ruficaudatus</i>	4	3.02	0.34	4	2.63	0.13
<i>Megaladapis edwardsi</i>	20	24.0	3.6	14	10.7	1.8
<i>M. grandidieri</i>	2	19.5	4.1	1	8.6	—
<i>M. madagascariensis</i>	1	20.9	—	nm ²	—	—

¹ Measurements in mm.

² nm, not measured.

In *Lepilemur* and *Megaladapis*, the postglenoid process is an inferiorly projecting extension of the temporal bone that is not continuous medially with the glenoid fossa (Fig. 2). In *Lepilemur*, its anterior surface is slightly convex in the coronal plane with a slight lipping either inferiorly or laterally. The postglenoid process in *Megaladapis* is a tear-shaped structure extending from the basicranium by a stout pedicle (Fig. 2B). Its anterior surface is moderately convex and its anterior-facing articular facet is roughly rectangular in shape.

The comparison of TMJ form to mode of ingestion and symphyseal strength in strepsirhines and ungulates shows that the presence of a posterior articular expansion and browsing are independent characteristics in ungulates (Table 4). However, a striking association between the presence of a posterior articular expansion and symphyseal morphology is apparent (Table 4 and Fig. 7). The maximum likelihood chi-square test is not significant for the mode of ingestion comparison ($\chi^2 = 2.02$, $P < 0.732$), but is highly significant ($\chi^2 = 17.33$, $P < 0.000$) for the symphyseal morphology comparison. With a few deviations (discussed in detail below) and irrespective of mode of ingestion, ungulates and strepsirhines with a fused or functionally fused symphysis have a posterior articular expansion and a corresponding articular facet on the postglenoid process.

DISCUSSION

The presence of thick articular tissue and an accessory articular meniscus in *Lepilemur* suggests significant amounts of move-

ment in addition to contact in the posterior TMJ. *Megaladapis* has an elongate, narrow, and concave posterior articular expansion compared to *Lepilemur*. This suggests enhanced congruence in the posterior TMJ and perhaps a greater range of motion in *Megaladapis*. However, in both genera, the convexity of the postglenoid process closely matches the concavity of the posterior articular expansion. The lack of association of a posterior articular expansion with browsing suggests that this joint design does not have a function during browsing. Moreover, there is a strong positive association between the posterior articular expansion and symphyseal strength. In both the strepsirhine and the ungulate samples, animals with a fused or functionally fused symphysis have a well developed posterior articular expansion compared to animals with an unfused symphysis. It is interesting to note that the koala bear (*Phascolarctos cinereus*) has a posterior articular expansion (Fig. 7) and a fused symphysis since *Megaladapis* converges on the koala bear in other aspects of anatomy that are related to feeding behavior (Table 1).

These observations support the transverse movement model, which postulates a functional relation between the posterior articular expansion, symphyseal fusion, large adductor muscle force, and large transverse jaw movements during the fast closing and power strokes of mastication. Experimental data are required to test this model.

What might cause relatively large transverse jaw movements? Transverse movements will be large if the occlusal angle of the postcanine teeth is parallel to the transverse plane (Lieberman and Crompton, 1996). In a comparative sample of mammals with fused and unfused symphyses, Lieberman and Crompton (1996) showed that symphyseal fusion is associated with a relatively flat occlusal angle. When the occlusal angle is flat, transverse muscle force must be used to produce transverse jaw movement since vertical muscle force is not effective (Becht, 1953; Greaves, 1980). Transverse jaw movements will also be large if anisodonty is great. Equids, rhinocerotids, and adapids show marked anisodonty (Fortelius, 1985), fuse the symphysis, and develop a posterior articular expansion.

TABLE 4. Comparison of posterior articular expansion and postglenoid facet associations in the Megaladapidae to ungulates and other strepsirhines

Taxon	Posterior articular expansion	Postglenoid facet expanded	Symphysis	Mode of ingestion	Diet category
Ungulata					
Hyracoidea					
<i>Procavia</i>	Absent	Absent	Fused	Graze	Herbivore
Perissodactyla					
Equidae	Present	Present	Fused	Graze	Herbivore
Rhinocerotidae	Present	Present	Fused	Graze and browse	Herbivore
Tapiridae	Intermed	Present	Fused	Browse	Herbivore
Artiodactyla					
Suidae					
<i>Babryrousa</i>	Present	Reduced	Fused	Browse	Omnivore
<i>Phacochoerus</i>	Present	Reduced	Fused	Browse and root	Herbivore
<i>Hylochoerus</i>	Present	Reduced	Fused	Browse	Herbivore
<i>Sus</i>	Present	Reduced	Fused	Root	Omnivore
Tayassuidae	Intermed	Present	Fused	Browse	Omnivore
Hippopotamidae	Intermed	Present	Fused	Graze	Herbivore
Camelidae	Present	Present	Fused	Graze and browse	Herbivore
Tragulidae	Absent	Absent	Unfused	Browse	Frugivore
Cervidae	Absent	Absent	Unfused	Browse	Herbivore
Giraffidae					
<i>Okapia</i>	Absent	Absent	Unfused	Browse	Herbivore
<i>Giraffa</i>	Present	Present	Fused	Browse	Herbivore
Antilocapridae	Absent	Absent	Unfused	Graze and browse	Herbivore
Bovidae	Absent	Absent	Unfused	Graze and browse	Herbivore
Extant primates ¹					
Megaladapidae					
<i>Lepilemur</i>	Present	Present	"Fused" ²	Browse	Folivore
<i>Megaladapis</i>	Present	Present	Fused	Browse	Folivore
Lemuridae	Absent	Absent	Unfused ³	Incise	Frugivore/folivores and insectivores
Hapalemuridae					
<i>Hapalemur</i>	Present	Present	Fused ²	Incise	Folivore
Indridae	Present	Present	Fused ²	Browse	Folivore/frugivore
<i>griseus</i>					
Galagidae	Absent	Absent	Unfused	Incise	Insectivore/Frugivore
Cheirogaleidae	Absent	Absent	Unfused	Incise	Insectivore/Frugivore
Lorisidae	Absent	Absent	Unfused	Incise	Insectivore/Frugivore
Extinct primates					
Adapidae					
Notharctinae					
<i>Cantius venticolis</i>	Present	Present	Fused	?	Frugivore
<i>Notharctus</i>					
<i>N. tenebrosus</i>	Present	Present	Fused	?	Folivore
<i>N. robustior</i>	Present	Present	Fused	?	Folivore
<i>Smilodectes gracilis</i>	Present	Present	Fused ⁴	?	Folivore
Adapinae					
<i>Adapis parisiensis</i>	Variable	Present	Fused	?	Folivore
<i>Leptadapis magnus</i>	Present	Present	Fused	?	Folivore

¹ Articular surface on the posterior aspect of the condyle in anthropoids is discussed in the text. When anthropoid families are included in the analysis, the maximum likelihood χ^2 is significant for the symphyseal morphology comparison ($\chi^2 = 12.44$, $P < 0.002$) and not significant for the mode of ingestion comparison ($\chi^2 = 4.72$, $P < 0.318$).

² The dentaries are inseparable in skeletal specimens of *Lepilemur* and fuse with age in the Indrids and *Hapalemur*. See also, Beecher 1977, 1979.

³ Beecher (1977) reports that *Lemur* (= *Eulemur*) *fulvus* and *L. macaco* show some ossification of the cruciate ligaments of the symphysis.

⁴ There is some disagreement in the literature. Ravosa (1996) describes the symphysis as partially fused, but Beecher (1983) describes the symphysis of *Smilodectes gracilis* as unfused.

See the text for results of the maximum likelihood χ^2 tests. Where only a family name is given, each genus available at the AMNH and SUNY-SB was surveyed. Suid and giraffid genera are listed separately because variation in one or more categories was present. Fused indicates partial or complete symphyseal fusion. "Fused" indicates functional fusion as defined in the text. Intermed indicates intermediate development of the posterior articular expansion.

There are several deviations from the association between fusion or functional fusion of the symphysis and the posterior articular expansion among primates and

ungulates. However, all of these may be explained by compromise in TMJ structure for some other behavior or structural modifications of the feeding apparatus indicating

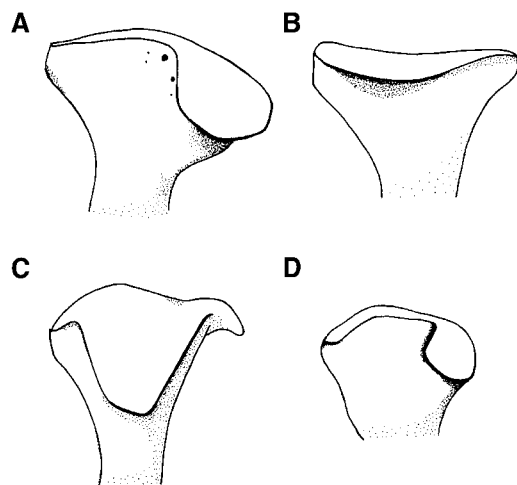


Fig. 7. Examples of the posterior aspect of the left condyle in the comparative sample (medial is to the right and superior is toward the top of the page). **A:** Horse (*Equus caballus*). **B:** Cow (*Bos bison*). **C:** Camel (*Camellus bactrianus*). **D:** Koala bear (*Phascolarctos cinereus*).

reduced amounts of transverse jaw movement.

A number of anthropoid species have a posteriorly expanded articular surface on the mandibular condyle (e.g., *Papio*, Fig. 1). Structural variation is substantial, but the anthropoid type of posterior articular expansion is confluent with the superior surface of the condyle and the junction of these surfaces is rounded. The available anatomical and experimental evidence indicates that the condyle does not contact the postglenoid process during mastication in anthropoids (Carlson et al., 1980; DuBrul, 1980; Wall, 1995), although there is a period of time during the power stroke when the balancing-side condyle moves posteriorly (Hylander et al., 1987). Based on cineradiographic recordings of wide gapes in several anthropoid species, Wall (1995) suggests that the posterior articular surface contacts the articular fossa or preglenoid plane during wide gapes, either to accommodate large food objects between the teeth or during canine display behaviors. Yet anthropoids have fused symphyses. The presence of symphyseal fusion and the absence of a posterior joint contact and movement is consistent with the transverse movement model if transverse jaw movements are relatively small in anthro-

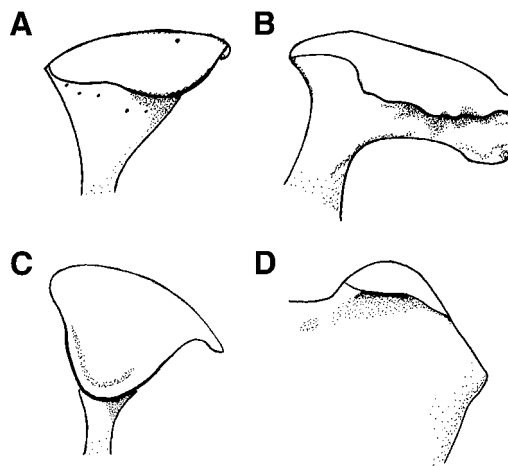


Fig. 8. The modified posterior articular expansions of *Tayassu*, *Hippopotamus*, and *Sus*. **A:** *Tayassu tajacu*, left side, posterior view with medial to the right. **B:** *Hippopotamus amphibius*, left side, posteromedial view with medial to the right. **C:** *Sus scrofa*, left side, posterior view with medial to the right. **D:** *Sus scrofa*, left side, lateral view with posterior to the right and showing oblique orientation of the posterior expansion. Superior is toward the top. See text for discussion.

poids as compared to ungulate and strepsirhine herbivores that have teeth that are strongly anisodontic and specialized for transverse shearing. Alternatively, anthropoids may have a posterior joint contact during mastication which has not been detected in cineradiographic recordings (cf. Murphy, 1956).

As shown in Figure 8, although a posterior articular expansion is present in peccaries (*Tayassu*) and hippopotamuses (*Hippopotamus*), it is rounded and generally more similar to what is seen in *Papio* (Fig. 1) than in other ungulates with a fused symphysis (Fig. 7). Work by Herring (1975) demonstrates that there are a variety of morphological correlates to the remarkably wide gapes that these species achieve during canine threat (*Hippopotamus*) and combat (*Tayassu*). It may be that *Hippopotamus* and *Tayassu* modify the posterior articular expansion to allow for greater jaw rotation about a coronal axis during wide gapes.

Procavia, the rock hyrax, does not fit the model because it shows no evidence of a posterior articular expansion. However, *Procavia* has a fused symphysis and transverse jaw movement during mastication (Janis,

1979). As with *Hippopotamus* and *Tayassu*, the TMJ of *Procapra* may be modified for large display gapes.

Compared to other perissodactyls, tapirs (*Tapirus*) have a less well developed posterior articular expansion (Table 4), perhaps because of a lack of emphasis on transverse dental movements during chewing. This is suggested by the bilophodont molar morphology (Osborn, 1981; Janis and Fortelius, 1988) and the greater amount of non-fibrous foods included in the diet (MacDonald, 1984).

The suid genera also differ from the expected condylar morphology. In suids, the posterior articular expansion lies at an obtuse angle to the superior surface of the condyle rather than at a 90 degree angle (Fig. 8), and on dry skeletons does not appear to articulate closely with the reduced postglenoid process. Herring and Scapino (1973) and Herring (1976) have shown that suids diverge from the ungulate chewing pattern because of a more omnivorous diet and a concomitant increased emphasis on crushing rather than transverse shearing/grinding movements. One or both condyles may experience posterior joint contact during chewing but perhaps minimal sliding motion occurs in the posterior part of the TMJ.

In regard to using the posterior articular expansion as a taxonomic character, the results of this study suggest that, although some minor shape differences are apparent, the posterior articular expansion is probably a synapomorphy that unites *Lepilemur* and *Megaladapis*. Character states that have been identified for the TMJ by Schwartz and Tattersall (1979, 1987) are given in Table 5. Character states defined in this study are given in Table 6.

As noted by Hill (1953), the indrids are distinguished from other strepsirrhines by the extreme expression of the posterior articular expansion and the postglenoid facet (Figs. 1 and 2). The posterior articular expansion is very large and angled slightly cranially relative to the coronal plane. The postglenoid process is appressed to the surrounding bone, creating a wall posterior to the condyle. The notharctines have a similar arrangement of the postglenoid process, but they are unique in the structure of the

TABLE 5. Character states identified previously for the TMJ in some living and fossil strepsirrhines

Condyle character states	
Schwartz and Tattersall (1979)	
Lemuridae (<i>Lemur</i> + <i>Varecia</i> + <i>Eulemur</i>)	1 "primitive"
Indridae	2
<i>Hapalemur</i>	3, polymorphic with 1
<i>Lepilemur</i>	3
<i>Megaladapis</i>	3
<i>Pelycodus</i> (<i>Cantius</i>) (AMNH 15019)	3, less pronounced
<i>Notharctus</i> (AMNH 21960, 21864, 13230)	3
<i>Smilodectes</i> (USNM 17995, 21815)	3
<i>Adapis</i> (BMNH 1633, 7506)	3

"(1) the primitive condition, as seen in *Lemur*, in which the condyle is broad transversely, and the somewhat posteriorly directed articular facet is distinct from, rather than confluent with, the posterior surface of the condylar neck; (2) a derived condition seen in the indrids, in which the condyle may be broad transversely, but is also more or less strongly curved in the coronal plane, and where the articular facet is confluent with the posterior aspect of the condylar neck; (3) a different derived condition . . . in which a distinct articular facet descends, medial to the condylar neck, from the posterior aspect of the transversely broad condyle." (p. 276)

Condyle articular surface shape	
Schwartz and Tattersall (1987)	
Lemur group (+ <i>Hapalemur</i>)	Straight
<i>Lepilemur</i>	"Lip"
<i>Daubentonina</i>	Arcuate
Indridae	Arcuate
<i>Pelycodus</i>	"Lip"
<i>Notharctus</i>	"Lip"
<i>Smilodectes</i>	Straight
Adapidae <i>sensu stricto</i> ¹	Arcuate

¹ Comprises *Adapis*, *Leptadapis*, *Paradapis*, *Alsatis*, and *Simonsia*.

posterior TMJ (Fig. 3). Not only is the posterior articular expansion very convex, it has a substantial cranial angulation relative to the coronal plane.

Besides the *Lepilemur*/*Megaladapis* comparison, the only extant-fossil comparison that yields a significant similarity in design is that between *Hapalemur*, *Adapis*, and *Leptadapis* (Fig. 3). The condyles of the Eocene adapids examined in this study do not bear a close structural resemblance to those of megaladapids or indrids, nor do the condyles of notharctines resemble those of adapines (Figs. 1, 2, and 3), even though the results of this study indicate a similar function in all groups.

TABLE 6. Character states defined in this study

Taxon	Temporomandibular joint character states
<i>Lemur</i> + <i>Eulemur</i> + <i>Varecia</i>	1
<i>Hapalemur</i>	4, polymorphic with 1
<i>Lepilemur</i>	3
<i>Megaladapis</i>	3
Indridae	
(<i>Propithecus</i> + <i>Avahi</i> + <i>Indri</i>)	2
<i>Cantius venticolis</i> (AMNH 14656)	5
<i>Smilodectes gracilis</i> (USNM 21815, 25686, 33–67)	5
<i>Notharctus tenebrosus</i> (USNM 21864, 21968; AMNH 11466a, 127167, 93617)	5
<i>Adapis parisiensis</i> (AMNH 98203, 99982)	4
<i>Leptadapis magnus</i> (MNHM 10893)	4

(1) As in Schwartz and Tattersall (1979). In addition, the superior surface of the condyle is more or less straight and there is no contact between the mandibular condyle and the postglenoid process. (2) As in Schwartz and Tattersall (1979). In addition, the posterior articular expansion is at an oblique angle relative to the superior surface of the condyle, an articular facet is present on the postglenoid process, and the postglenoid process forms a bony wall with the entoglenoid process and the auditory bulla. (3) As in Schwartz and Tattersall (1979). In addition, the superior surface of the condyle is straight in *Lepilemur* but concavo-convex in *Megaladapis*, the posterior expansion is set at approximately 90 degrees to the superior surface of the condyle, an articular facet is present on the postglenoid process, and the postglenoid process does not form a bony wall with the entoglenoid process and the auditory bulla. (4) A short, though distinct, articular facet descends medial to the condylar neck on its posterior surface. This feature is polymorphic in *Hapalemur* (with character state 1) and variable in size in *Adapis* and *Leptadapis*. In addition, the superior surface of the condyle is straight, the posterior articular expansion is set at approximately 90 degrees to the superior surface of the condyle, an articular facet is present on the postglenoid process, and the postglenoid process forms an incomplete bony wall. (5) A posterior articular surface that is confluent with the superior surface of the condyle descends medial to the condylar neck. This surface is highly convex in the sagittal and coronal planes and is set obliquely relative to the superior condylar surface. An articular facet is present on the postglenoid process, and the postglenoid process forms a bony wall with the entoglenoid process and the auditory bulla.

There is independent evidence that the strepsirhines that express the posterior articular expansion are (or were) folivorous (Covert, 1986, 1990) and emphasized molar shear during transverse tooth movement. The correlation between joint shape and folivory lends support for a similar function in all of the primate subfamilies. However, *Cantius* (= *Notharctus*) *venticolis* violates the transverse movement model as a purported frugivore (Covert, 1986), although it is possibly descended from a folivore (Covert, 1990). It should also be noted that in one specimen of *Notharctus robustior*

(AMNH 12567), the postglenoid facet was weakly developed.

The comparative results demonstrate that the posterior articular expansion can evolve convergently. Indeed, structural differences in both the posterior articular expansion and the postglenoid process argue strongly for convergence within ungulates and strepsirhines. Therefore, these traits are not reliable as synapomorphies when used to unite families and/or subfamilies of strepsirhines.

CONCLUSIONS

The posterior articular expansion and the postglenoid facet of megaladapids are an adaptive convergence with ungulates in response to similar functional demands placed on the feeding apparatus in the two groups. Other folivorous strepsirhines with a fused or functionally fused symphysis have a posterior articular expansion and a postglenoid facet, and it is suggested that these features have a similar function to those of ungulates and megaladapids during mastication. It is proposed that the posterior articular expansion and the postglenoid facet provide a movement surface that helps to guide the condyles during extensive transverse jaw and tooth movements, on the working-side during fast closing and on the balancing-side during the power stroke. The convergence in ungulate and strepsirhine TMJ morphology does not refute Tattersall's (1972) browsing hypothesis.

None of the strepsirhine species examined displays a TMJ configuration that is similar enough structurally to be considered synapomorphic with that of the Megaladapidae. The posterior articular expansion is linked to diet and evolves with structural changes elsewhere in the feeding apparatus, particularly the teeth and the mandibular symphysis. On this basis, it seems reasonable to suggest convergent evolution among primate families and subfamilies in which similar diets and tooth movements occur (e.g., folivory in notharctines, adapines, megaladapids, hapalemurids, and indrids).

ACKNOWLEDGMENTS

I thank Elwyn Simons (Duke University) for providing the opportunity to work in Madagascar in the summer of 1991, and also

Berthe Rakotosamimanana (L'Université d'Antananarivo) for permission to study the *Megaladapis* material at the Service de Paléontologie. Ross MacPhee (AMNH, Mammalogy), Guy Musser (AMNH, Mammalogy), and Ken Glander (Duke University) very generously permitted the dissection of *Lepilemur* cadavers in their care. Wolfgang Fuchs (AMNH, Mammalogy), John Alexander (AMNH, Vertebrate Paleontology), and Robert Emry (USNM, Vertebrate Paleontology) provided access to specimens in their care. John Alexander prepared USNM 21815 so that both mandibular condyles could be seen for the first time. A preliminary version of this research was presented at the 1992 American Association of Physical Anthropologists annual meeting. A special thanks to Bill Jungers for providing me with some of the *Megaladapis* measurements, to both he and Laurie Godfrey for useful discussion of methods and results, and to D.E. Lieberman and A.W. Crompton for providing me with an advance copy of a manuscript on jaw movements in goats. I also want to thank Bill Hylander, Blythe Williams, Daniel Schmitt, three anonymous reviewers, and the associate editor for making helpful comments and criticisms that greatly improved the manuscript. This study was supported by a National Science Foundation Graduate Fellowship (to the author) and NSF BNS-8911315 (to Elwyn Simons).

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